

REPRODUCTIVE PHYSIOLOGICAL VARIATION IN LATITUDINALLY SEPARATED POPULATIONS OF THE BAY SCALLOP, *AEQUIPECTEN IRRADIANS* LAMARCK ¹

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Populations of marine animals exposed to different environments within their geographical range may vary in physiological properties. Bullock (1955), Prosser (1955) and Vernberg (1962) reviewed the earlier literature on this subject and discussed the importance of physiological differences in the study of distribution, acclimation and speciation. In many of these studies physiological differences have

TABLE I
The mean size and the mean body weight of monthly samples of scallops analyzed for determination of the reproductive activity

Month	Woods Hole, Massachusetts		Beaufort, North Carolina	
	Size mm mean $\pm$ S.D.	Body weight g mean $\pm$ S.D.	Size mm mean $\pm$ S.D.	Body weight g mean $\pm$ S.D.
1965				
January	61.33 $\pm$ 3.57	16.91 $\pm$ 5.23	71.01 $\pm$ 4.52	38.87 $\pm$ 7.60
February	61.55 $\pm$ 3.40	18.68 $\pm$ 5.69	30.00 $\pm$ 6.22	2.62 $\pm$ 1.97
March	42.71 $\pm$ 3.44	5.44 $\pm$ 1.33	27.50 $\pm$ 3.42	1.82 $\pm$ 1.35
April	43.33 $\pm$ 1.99	4.82 $\pm$ 1.68	26.35 $\pm$ 6.89	1.75 $\pm$ 1.45
May	53.71 $\pm$ 8.83	9.59 $\pm$ 5.99	31.43 $\pm$ 0.44	1.90 $\pm$ 0.17
June	57.97 $\pm$ 11.86	14.05 $\pm$ 9.39	33.47 $\pm$ 4.36	3.57 $\pm$ 1.41
July	49.28 $\pm$ 2.39	8.22 $\pm$ 0.81	49.35 $\pm$ 5.24	10.00 $\pm$ 3.04
August	52.77 $\pm$ 5.22	8.51 $\pm$ 1.96	62.18 $\pm$ 3.54	22.23 $\pm$ 3.92
September	59.11 $\pm$ 6.02	11.32 $\pm$ 2.87	62.41 $\pm$ 4.22	22.05 $\pm$ 3.55
October	56.09 $\pm$ 3.42	11.62 $\pm$ 2.77	62.19 $\pm$ 7.05	20.41 $\pm$ 1.97
November	62.73 $\pm$ 5.56	25.44 $\pm$ 6.20	56.15 $\pm$ 4.60	15.25 $\pm$ 2.89
December	49.53 $\pm$ 4.05	8.06 $\pm$ 2.25	51.03 $\pm$ 5.71	10.45 $\pm$ 3.05

been compared by measuring rate processes such as oxygen consumption and heart beat. Population differences in resistance to environmental extremes have also been demonstrated for marine animals (Vernberg, 1962). More recently, progress has been made in understanding the mechanisms of temperature acclimation (Prosser, 1967; Troshin, 1967).

The geographical range of a species is regulated by the environmental limits for its survival, functioning and reproduction (Hutchins, 1947; Spark, 1957). Varying adaptive capacities of populations exposed to different environments may serve as a primary mechanism in speciation (Prosser, 1960; Mayr, 1963). The reproductive physiological response of populations exposed to different environments

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within the overall range of a species has been examined for few marine animals. Consequently, the adaptive mechanisms for reproduction in different environments and their role in the speciation process are not well understood.

The bay scallop, *Aequipecten irradians* Lamarck, has a wide distribution along the Atlantic and Gulf Coasts of the United States, resulting in many separate populations exposed to different environments (Abbott, 1954; Schroeder, 1966). Populations of this species in different parts of the range vary in the timing of the spawning period (Sastry, 1963). The present study examines the annual reproductive activity of populations of scallops occurring in different temperature environments. The effects of food and temperature on the reproductive response of scallops have been investigated in a series of laboratory experiments, the results of which were reported earlier by Sastry (1966a, 1968).

MATERIALS AND METHODS

Populations of *A. irradians* examined in the present study were collected in the Falmouth area of Nantucket Sound near Woods Hole, Massachusetts and off Beau-

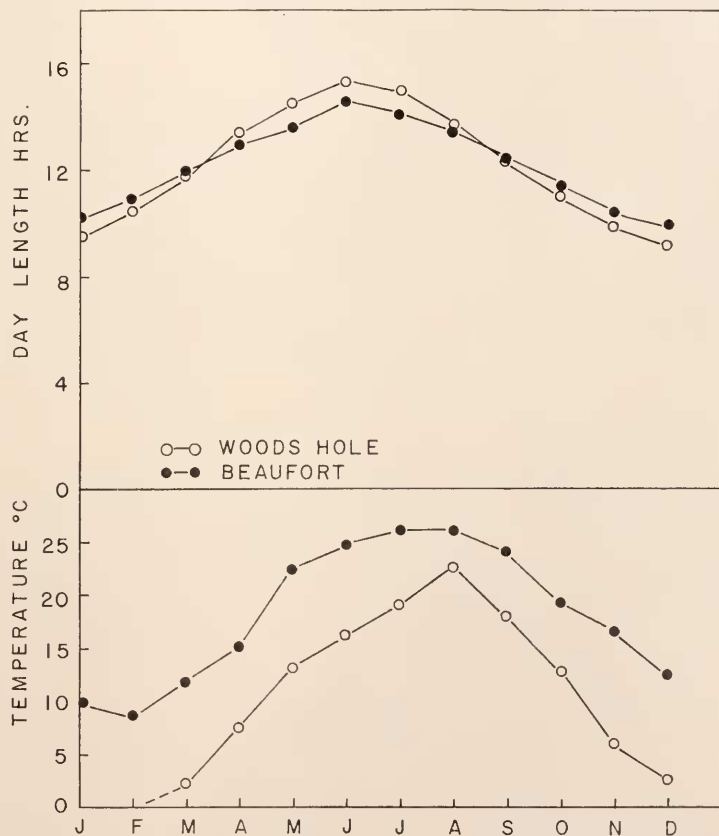


FIGURE 1. Monthly mean sea water temperature and the average day-length in the geographical locations where the scallops were collected.

fort, North Carolina (Table I). The two populations are exposed to significantly different environmental temperatures throughout the year (Fig. 1). Monthly samples collected near Woods Hole were flown live in chilled containers to Beaufort for analysis. The Beaufort scallops were collected near the Duke University Marine Laboratory.

The population samples were analyzed to determine the monthly gonad index (gonad weight/body weight $\times 100$), digestive gland index (digestive gland weight/body weight $\times 100$) and the stage in gametogenesis according to the methods

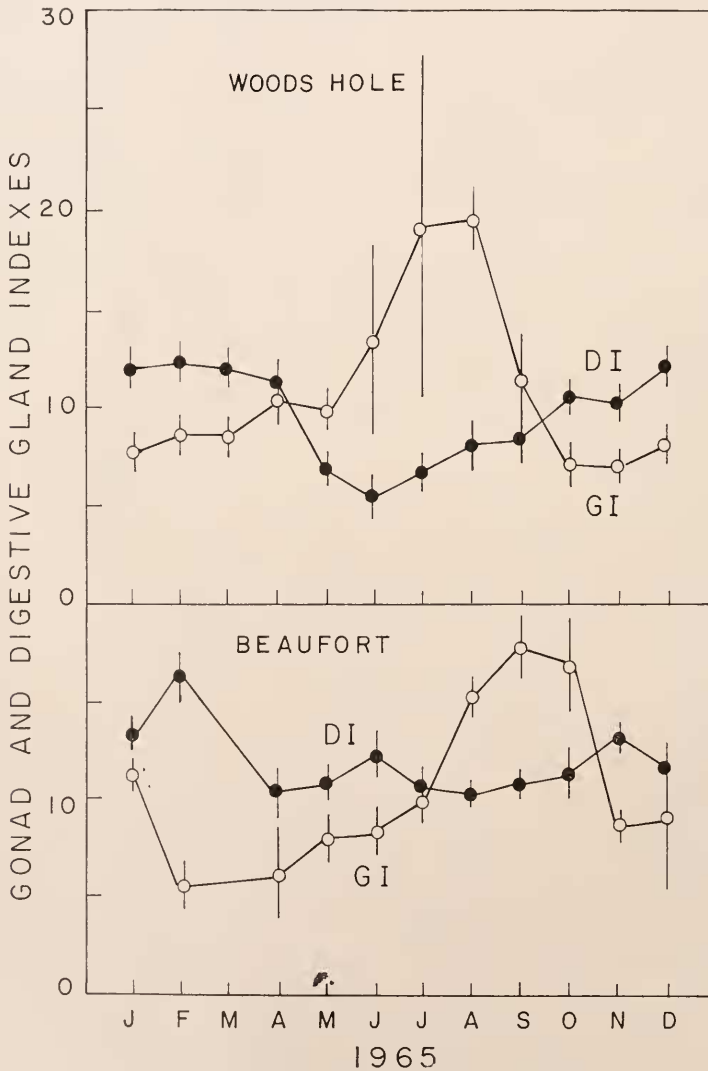


FIGURE 2. Observed monthly mean gonad and digestive gland index values for the populations of scallops from Woods Hole, Massachusetts and Beaufort, North Carolina. Vertical lines show the 95% confidence intervals from the mean.

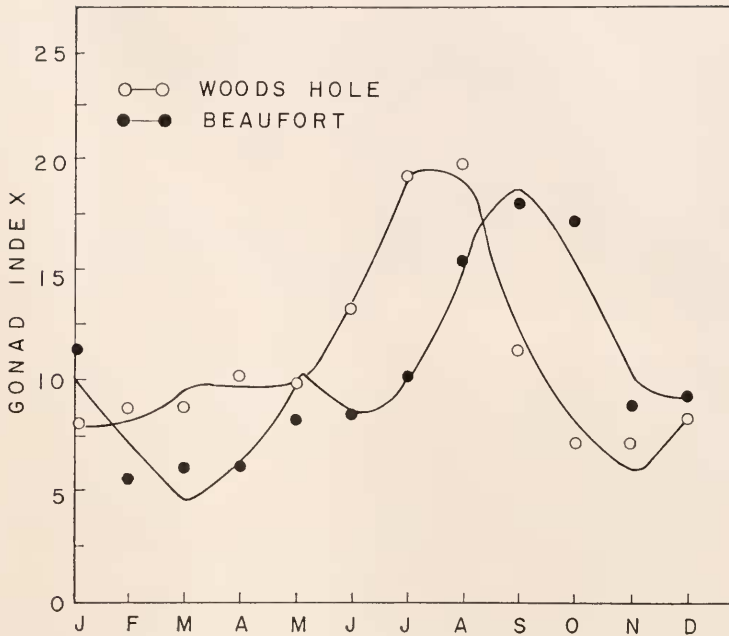


FIGURE 3. Monthly mean gonad index values for the populations of scallops fitted with the three-term Fourier curves show a cyclical trend in gonad activity response within the twelve month period.

described by Giese (1959) and Sastry (1966a). The observed monthly gonad index values were fitted with an annual trend line determined by the method of periodic regression analysis described by Bliss (1958).

OBSERVATIONS

Annual gonad cycle

The monthly mean gonad index values for the two populations of scallops are shown in Figure 2. The three-term Fourier curves fitted to the observed data clearly show the cyclical gonad activity of the populations during the year (Fig. 3). The annual gonad cycle of the scallops includes vegetative, growth and gametogenesis, maturation, spawning, and resting periods (Sastry, 1966a), but these stages are reached at different times in the two populations. Gonad growth takes place from April through July at Woods Hole, from June through September at Beaufort. The duration of gonad growth activity is approximately the same for both populations. The gonad index seems to decrease with the onset of spawning (Sastry, 1966a). The Woods Hole population has completed spawning by September, the time of the maximum gonad growth at Beaufort.

Relationship between the changes in gonad and digestive gland indexes

In the annual cycle, gonad growth seems to occur by an accumulation of nutrient reserves in the tissue which are apparently utilized by the developing gametes for

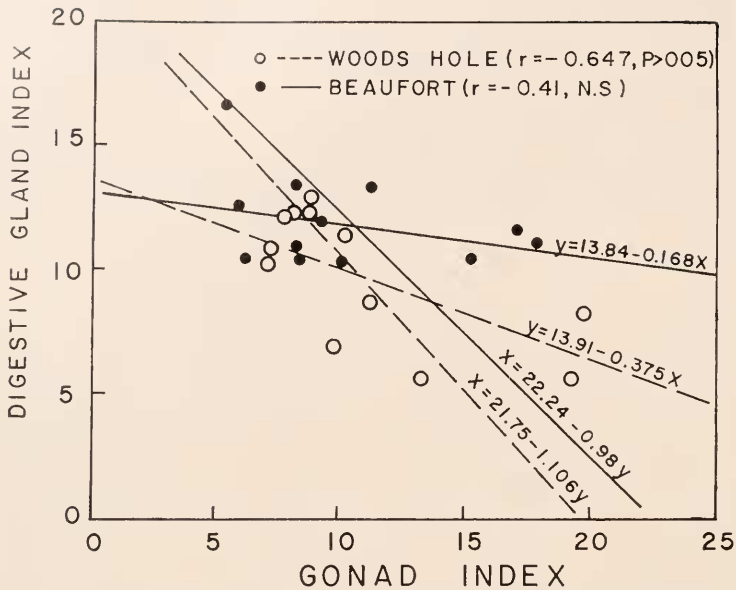


FIGURE 4. Correlation between monthly mean gonad index and the digestive gland index of the populations of scallops.

synthesis of various biochemical constituents (Marshall and Orr, 1961; Giese, 1959; Barnes, Barnes and Finlayson, 1963; Sastry, 1966a, 1968). The changes in the monthly gonad and digestive gland indexes in some marine invertebrates show a reciprocal relationship suggesting the influence of food on gonad growth (Giese, 1959; Sastry, 1966a, 1968). The digestive gland index of the scallop populations is at a relatively higher level than the gonad index during the vegetative and resting periods (Fig. 2). To determine the significance of the relationship, correlation coefficients were computed. Both populations showed a negative correlation, but this was significant at the 5% probability level only for the population at Woods Hole (Fig. 4). The changes in the monthly digestive gland index probably indicates the amounts of nutrient reserves in the tissue which vary with gonad growth activity and seasonal changes in the environment. In a number of laboratory experiments, it has been shown that scallops in the resting stage require abundant food and exposure to minimum temperature to begin gonad growth (Sastry, 1968). The nutrient reserves present in the digestive gland, however, are obviously not adequate to sustain gonad growth. Continuing growth is apparently related to periods of abundant food production.

Gametogenesis

The predominant stages in gametogenesis observed in the two populations of scallops are given in Table II. Similar stages in gametogenesis appear in both populations during different months of the year. The Woods Hole population develops oögonia by March, and the oocytes begin the synchronous growth phase

during April. Vitellogenesis is underway in May, and by late June the oocytes have begun to mature. Fertilizable eggs are present from the middle of July through August. The gonads are neutral from September to December.

The Beaufort population also develops a few oogonia by March and the oocytes are in the synchronous growth phase in April. These oocytes complete vitellogenesis during May, but they disintegrate before becoming fertilizable eggs. However, at this time the population again develops oogonia, in larger numbers than before. The oocytes developed by June begin the synchronous growth phase. Vitellogenesis begins in July, and the oocytes become fertilizable eggs by late September. The population is in a mature reproductive state from then until the middle of November.

TABLE II

The predominant stages in gametogenesis observed in the populations of scallops during different months of the year*

Stage in gametogenesis	Woods Hole, Massachusetts	Beaufort, North Carolina
Oogenesis		
Primary germ cells	January–February	January–April
Oogonia	March	May
Synchronous oöcyte growth	April–May	June–July
Vitellogenesis	May–June	July–September
Fertilizable eggs	July–September	September–November
Spermatogenesis		
Spermatogonia	January–March	January–April
Spermatocytes	April–May	May–June
Spermatids	June	July–August
Spermatozoa	July–September	August–November
Neutral gonads	September–December	Late November–December

* A detailed description of the stages in gametogenesis of scallops is given by Sastry (1966a).

The monthly mean oocyte diameter is shown in Figure 5. The monthly oocyte growth rates for the two populations were compared by the method of analysis of covariance (Snedecor and Cochran, 1967). The oocyte growth rate in the Woods Hole population ($Y = 9.92 X - 3.31$) was higher than in the Beaufort population ($Y = 7.0 X - 3.9$).

Statistical analysis of variation in the annual reproductive cycle of the populations

The three-term Fourier curves fitted to show the cyclical gonad activity are described by the following periodic regression equations:

$$Y = 11.03 - 4.6631 u_1 + 0.03927 v_1 + 2.6816 u_2 + 1.51242 v_2 - 1.003 u_3 - 1.4883 v_3 \quad (\text{Woods Hole}); \text{ and}$$

$$Y = 10.36 - 2.0101 u_1 - 4.5021 v_1 - 0.500 u_2 + 1.2925 v_2 + 2.1416 u_3 + 0.0533 v_3 \quad (\text{Beaufort}).$$

In these equations, the first term describes the fundamental cycle (sine curve) for the year. Addition of the remaining two terms recovers the curves fitted for the observed data. The variation in the regression coefficients in the first term of

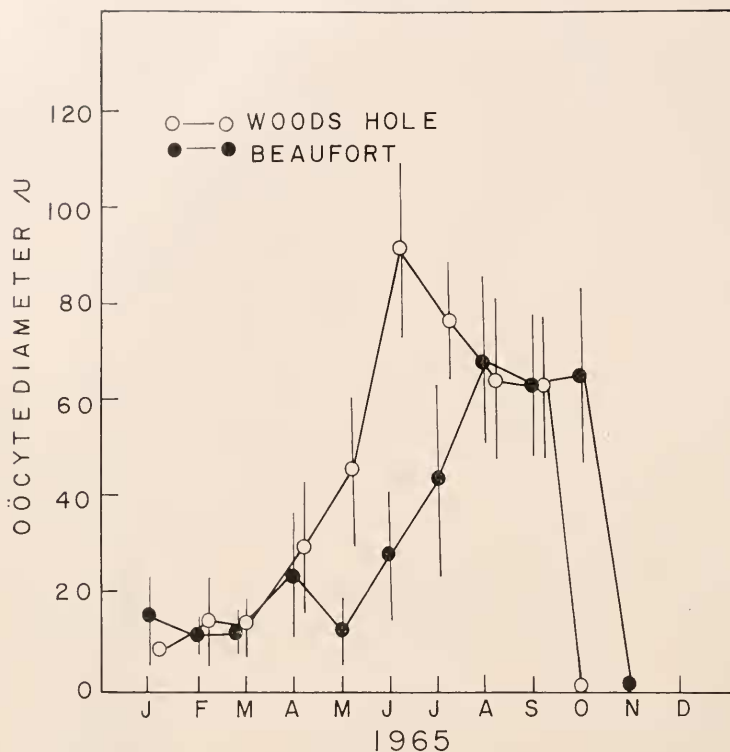


FIGURE 5. Observed monthly mean oocyte diameter for the populations of scallops. Vertical lines show 95% confidence intervals from the mean.

the two equations indicates a possible difference in amplitude, in phase angle (time of maximum) or both (Bliss, 1958). The estimated amplitude of gonad response for the two populations is approximately the same (Woods Hole, 9.32; Beaufort, 9.80). However, the maximum amplitude occurs about June 25 at Woods Hole and August 19 at Beaufort. This displacement is probably the most significant difference between the annual gonad activity cycles of the two populations. The difference is apparently due to the two populations interacting in the same way with different conditions of temperature and food abundance.

DISCUSSION

Physiological variation in populations of a species exposed to different environments could be either a phenotypic response of a single genotype or could be truly genetic (Prosser, 1955). Genetic divergence of populations may bring differences in adaptive capacities and thus serve as a mechanism in species differentiation. Comparison of physiological responses of some geographically separated populations of marine animals has shown variation in adaptive capacity, but in many cases the difference has been phenotypic.

The processes examined in the earlier studies are directly related to the survival of adult organisms in the different environments, but reproductive physiological activity is concerned with species continuity. Variation in reproductive activity may therefore be adaptive for continuity of populations in geographically separated areas. It may thus become significant in evolutionary divergence.

The reproductive physiological process is a cyclical activity that may be repeated on an annual, semi-annual or continuous basis (Giese, 1959). The pattern of annual reproductive activity may be considered as a genetically controlled response to the environment. This is seen clearly in some marine invertebrates in temperate zones. Successive events in the reproductive cycle correlate with differences in the environment that develop during the year. Thus, a succession of environmental factors influences the events in the annual reproductive cycle. It is possible that the timing of reproductive events may have to be coordinated with the seasonal changes in the environment to exhibit the characteristic cycle of annual gonad activity. The temperatures corresponding to the successive events in the reproductive cycle are lower at Wood Hole than at Beaufort (Figs. 1 and 2). Ryther and Yentsch (1958) and Yentsch (1963) reported that phytoplankton production reached peak levels during the winter and spring in Northern locations. At Beaufort, the phytoplankton production peaks during the summer months (Williams and Murdoch, 1966). Thus, the displacement of reproductive events of the populations may have been favored by selection as an adaptive response to geographical differences in the period of abundant food production and temperatures.

To determine whether variation in annual reproductive activity of scallops is genetic or environmental, acclimation tests will have to be performed (Prosser, 1955; Sastry, 1966b and Sastry, unpublished observations). The basis of variation among geographically separated populations is not clear for most marine invertebrates. However, it has been suggested that the breeding period of a species occurs at characteristic temperatures which remain a constant throughout the geographical range (Orton, 1920). Runnstrom (1927) suggested that the breeding period of widely distributed marine animals is earlier in the southern part of their range, but at about the same temperatures as in the North. Although, temperature affects reproduction, other environmental factors appear to interact with it in determining the pattern of annual gonad activity in a given geographical area. It is likely the variation in annual reproductive activity of a species will be the phenotypic response of a single genotype. Alternately, however, the variation may result from genetic divergence of the populations in different parts of the range. In that case the populations would not reciprocally acclimate. Stauber (1950), Loosanoff and Nomejko, (1951), and Korringa (1957) observed that the critical minimum temperatures for spawning of geographically separated populations of *Crassostrea* and *Ostrea* were different and suggested that they might represent physiological races. The populations of scallops in the present study vary in the time of year when successive reproductive events take place and also in the environment for these events. It is possible that the variation in the populations of scallops could have been induced by their coordination of reproductive events with the environment at the whole organism level.

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SUMMARY

1. The geographically separated populations of the bay scallop *A. irradians* from Woods Hole, Massachusetts, and Beaufort, North Carolina, vary in their timing of reproductive events. These events occur earlier in the year at Woods Hole than at Beaufort.
2. The monthly gonad index values of the populations are fitted with three-term Fourier curves to show the cyclical trend of gonad activity response within the year. Periodic regression analysis of the data indicates that displacement of maximum gonad response is a significant difference between the two populations.
3. The reproductive physiological variation in the populations of scallops may have been favored through selection as an adaptive response to the geographical differences in temperature and time of abundant food production.
4. The variation could be either phenotypic or truly genetic.

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